QUANTITATIVE GENETICS PART II

Selection

Edited by

William G. Hill

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QUANTITATIVE GENETICS
PART II
Selection

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SERIES EDITOR'S FOREWORD

The study of any discipline assumes the mastery of the literature of the subject. In many branches of science, even one as new as genetics, the expansion of knowledge has been so rapid that there is little hope of learning of the development of all phases of the subject. The student has difficulty mastering the textbook, the young scholar must tend to the literature near his own research, the young instructor barely finds time to expand his horizons to meet his class-preparation requirements, the monographer copes with wider literature but usually from a specialized viewpoint, and the textbook author is forced to cover much the same material as previous and competing texts to respond to the user's needs and abilities.

Few publishers have the dedication to scholarship to serve primarily the limited market of advanced studies. The opportunity to assist professionals at all stages of their careers has been recognized by Hutchinson Ross and by a distinguished group of editors knowledgeable in specific portions of papers that demonstrate both the development of knowledge and the atmosphere in which that knowledge was developed. There is no substitute for reading great papers. Here you can learn how questions are asked, how they are approached, and how difficult and essential it is to obtain definitive answers and clear writing.

Dr. Hill has approached one of the most difficult areas of genetics. Significant literature covers well over a century of writing, and the interaction of this field with the development of statistical theory, plant and animal breeding, and biochemical and molecular biological approaches results in a complexity difficult for observers from other fields to appreciate. The field is important to modern food production, to health care, and to the social sciences; moreover, it provides a basis for much of the theoretical understanding of evolutionary processes. In the first volume Dr. Hill gives us an understanding of the basis of quantitative variation, and in the second he chooses from the extensive literature on selection experiments. I find it exciting to reread these papers with his commentary at hand. His scholarship will be appreciated by his colleagues.

DAVID L. JAMESON

PREFACE

This volume is Part II of a collection of Benchmark Papers in Quantitative Genetics. In Part I, "The Explanation and Analysis of Continuous Variation," I pointed out that the original intention was to produce a single volume, but that I found it impossible to span the field adequately in the limited space. The papers in Part I, which essentially deal with the static description of populations in quantitative genetic terms, are intended to serve as groundwork for the papers on selection that are included here. The papers chosen for this volume are substantially more recent, and I have paid less attention to the historical development. No doubt, for some tastes, the reprints are still too old (this is not molecular biology); perhaps for others, too young. I hope the reader finds them all interesting.

My intention has been to cover both the theoretical basis and some of the experimental results and to feature as many as possible of the major workers. Perhaps my own interests and prejudices show through in the preponderance of papers on theory and on animals, but studies are included that show that the predictions actually work in practice. Fortunately, I have been able to include a greater number of papers than in the first volume, and I hope I have achieved some breadth of coverage. Even so, only lengthy excerpts could be taken from a few, and there are many more papers I would have liked to include—indeed, whole books. The choosing was always an interesting problem.

I again wish to acknowledge many people for their help: David Jameson for inviting me to prepare these collected papers and for his advice; the authors and publishers for permission to reprint their material and, in the case of many authors, for helpful comments; Douglas Falconer and Joe Felsenstein for criticism and advice on the manuscript; and Jackie Bogie for her excellent typing of it. I am especially grateful to my many colleagues, who provide such a stimulating environment in Edinburgh and who have acted as constructive sounding boards for my suggestions of papers.

WILLIAM G. HILL

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INTRODUCTION

The study of selection of quantitative traits encompasses both evolution by natural selection and improvement of domestic plants and animals by artificial selection. Although evolution may have proceeded by periods of rapid change followed by near stasis, the major traits have presumably always shown continuous or nearly continuous distributions, and there remain substantial overlaps of distribution among species. The power of selection to change a population, if not to develop new species, has been convincingly demonstrated by experimentalists and breeders; a few generations can suffice to change a population to a new mean level well outside its original range.

Part I of these volumes of Benchmark Papers in Quantitative Genetics, "The Explanation and Analysis of Continuous Variation," dealt with the evidence, the historical development, and the acceptance of the multifactorial Mendelian model, and in particular with prediction of the correlation among relatives. Those results are an essential background for the discussions of selection. As a consequence, although papers in Part I were taken only to the mid-1960s, more recent papers are included here, with less concentration on the early historical development. Another, more fortunate difference between the volumes is that the papers that represent important contributions to selection were, on average, shorter than those in other areas, so rather more papers are included. Even so, they cannot be expected to include *all* the notable developments.

Evidence for the effectiveness of selection came from two quite different sources. The first was implicit: the apparent ability of natural selection to produce new modifications and to increase adaptation, leading to Darwin's and Wallace's theories of evolution. The second was more explicit: the experiments of Castle and colleagues (Paper 1), the Illinois corn oil study, and many others showed that substantial changes in a population could occur, even though Johannsen and others such as Jennings (Paper 2) had been unable to get responses in pure lines. There were alternative explanations: changes to new variants occurred by mutation, or responses were due simply to increases in frequency of favorable genes. It is obvious to us now that both causes are major contributors, the relative importance depending on the time span of the selection, but the topic generated substantial debate. The general resolution of the differences, in favor of changes in frequency, occurred by about 1920, and is discussed in the papers of Sturtevant (Paper 3) and Castle (Paper 4). These papers are included in the first section, "Nature of Selection Response," and they put selection into the multifactor Mendelian framework that by then was essentially accepted as an explanation of continuous distribution of quantitative traits, correlation among relatives, inbreeding depression, and heterosis, all topics considered in Part I.

There was, nevertheless, neither a theory for predicting responses to artificial selection practised in a population, nor any mathematical demonstration that natural selection could lead to substantial evolution of a population, nor any prediction of the rate at which it might occur. The major advances in the evolutionary context were made by Haldane, Fisher, and Wright, culminating in their publications of the early 1930s (Fisher, 1930; Haldane, 1932; Wright, 1931). It is not, of course, possible to reproduce these works in full in the present volume, but an attempt is made to give a flavor of their studies by including particular aspects most closely related to the inheritance of quantitative traits. Most of the major developments in the context of applications to artificial selection were made by workers concerned with animal breeding.

Prediction equations in quantitative genetics can be at two levels: those based on changes of gene frequency at individual loci, perhaps then summed over loci to show changes in the trait, and those based essentially on regressions of progeny on parent performance assuming, for example, each is normally distributed. The necessary statistics for the latter, such as heritability, do not require any knowledge of the numbers, effects, and frequencies of genes influencing the trait. Predictions can be based on quantities observed directly in the population, but are of value only so long as heritability, for example, remains constant. Since selection, by changing gene frequencies, must change heritability, this latter assumption would seem invalid, but in practice it usually holds well for a number of generations. In large animals with slow generation turnover this time is plenty long enough for the formulae to be useful.

Papers in which selection theory is developed at the statistical level, in terms of variances, covariances among relatives, heritabilities, and regressions, are therefore included in Section II, "Statistical Predictions of Selection Theory," while those dealing primarily with changes at the individual locus level are deferred to Section III, "Genetical Predictions of Selection Response." The ordering is somewhat arbitrary, but the statistical papers inherently deal with the more short-term problems. The topics covered span most of the major topics in the application of quantitative genetics to animal and plant breeding; however, because the developments have mostly been on the animal model, none that take their motivation directly from plant breeding problems are included. An important consideration is the relative efficiency of alternative methods of selection, classically of selection on individual performance versus selection on progeny performance. This problem is discussed by Lush (Paper 5), and Paper 8 by Dickerson and Hazel extends the analysis in an important way to consider the optimum rate to turn over generations. Obviously there is a trade-off between reducing the proportion selected and increasing the generation interval. In any improvement program there are multiple objectives, and the method for dealing with these as correlated traits in a selection index is described by Hazel in Paper 6. Falconer shows in Paper 7 how the ideas of genetic correlations can be extended to performance in different environments. Finally, Henderson, in Paper 9, reviews and develops what has become the integrating procedure for assessing the genetic merit of individuals, Best Linear Unbiased Prediction (BLUP).

Section III includes an abstract (Paper 10) from Fisher's (1930) book, *The Genetical Theory of Natural Selection,* on the fundamental theorem of natural selection. This is the most widely known formula in the application of quantitative genetics to evolution and has generated much research into its applicability. Regrettably, only that abstract and the short paper by Haldane (Paper 11) could be included from Fisher's and Haldane's pioneering work on evolution by natural selection, and Haldane's paper is of more important application in showing how artificial selection changes gene frequencies. The remaining papers in this section deal with two particular but important problems in artificial selection: Comstock, Robinson, and Harvey (Paper 12) show how overdominance can be utilized by reciprocal recurrent selection (RRS), and A. Robertson (Paper 13) discusses problems of selection limits due to fixation of genes in finite populations. These two papers broke new ground in the application of quantitative genetics to animal and plant improvement and stimulated much experimental work.

There is an extensive and still growing literature on selection experiments in quantitative genetics. In a steadily accumulating body of information, it is not obvious which contributions are the most important, for different experiments are never complete replicates of each other. The majority of those chosen for inclusion in Section IV, "Results from Selection Experiments," were conducted in the 1950s, when laboratory animals were being used to test quantitative genetic selection theory and as models for farm livestock in experiments on the inheritance of growth and reproduction. Indeed, all the experiments described in this section were carried out in institutions concerned with agricultural research.

Perhaps the best known single selection experiment is the Illinois corn oil project, which started before the turn of the century and still continues. It is represented here by a recent report by Dudley, Paper 14. The *Drosophila* experiments conducted by Mather (Paper 15) were important not just for their descriptive value, but because they led him to hypotheses about the nature of quantitative (biometrical) genetic variation and the relations among genes on the chromosome.

Poultry have been longest subjected to intense artificial selection in breeding programs based on quantitative genetic principles. Lerner and Dempster (Paper 16) were early exponents of the principles and conducted important experiments on poultry. They were among the first to identify problems of selective plateaux in farm animal populations, and the results are outlined in their paper. Problems of fitness-associated limits were also a notable feature of F. W. Robertson's and Reeve's thorough studies (reported by Robertson in Paper 17) on growth in *Drosophila*. A major aim of selection experiments is to investigate the nature of inheritance of traits of importance, of which the preceding are examples. Falconer's paper (Paper 18) on the genetics of litter size is a further example, in which results were obtained that were not predicted *a priori* by the theory because they depended on the biology of the specific trait under investigation.

Another major aim of selection experiments is to test the validity of quantitative genetic theory. Clayton, Morris, and A. Robertson (Paper 19) undertook a direct test of various aspects of the theory using *Drosophila*, and, fortunately, they found good agreement between expectation and observation. Bell, Moore, and Warren (Paper 20) used laboratory animals in model selection experiments to test the efficiency of alternative breeding programs, a nice example of an intermediate step in the path from theory to experiment to practice.

In Section V, "Selection and Maintenance of Genetic Variation," we return to theory—not to directional selection as in previous sections, but to interactions among loci and traits, and to the role of selection in the maintenance of variation. Paper 21 is a summary by Wright of his basic evolutionary views, written in 1932, discussing work he had just published in more detail and was subsequently to expand at much greater length. A. Robertson (Paper 22) reviews the relationships between metric characters and fitness and considers alternative models for maintaining variation for different kinds of traits. The papers of Bulmer (Paper 23) and of Lande (Paper 24) are concerned with the effects of selection on the amount of genetic variance a trait exhibits; in both studies many of the results are couched in terms of linkage disequilibrium. Bulmer's analysis applies to directional and to stabilizing selection and Lande's only to stabilizing selection, but Lande considers the balance between gain of variation by mutation and loss by selection. These papers have been important in stimulating interest in analysis of quantitative genetic variation by workers in evolutionary and ecological genetics.

The final section covers experimental results and techniques for predicting how much variation is produced by mutation, how variation is maintained by selection, and the numbers, effects, and locations in the chromosome of the genes affecting quantitative traits. Some of these problems have been touched on in earlier papers (e.g., those by Mather and F. W. Robertson), but the papers in Section VI, "Nature of Quantitative Variation," go into more detail. An estimate of the new variation arising from mutation is obtained by Clayton and A. Robertson (Paper 25). Direct evidence of the effect of stabilizing selection on reducing the fitness of extreme individuals is produced by Linney, Barnes, and Kearsey in Paper 26 (data on this topic are much less numerous than models). The Illinois corn oil experiment was mentioned previously, and as early as 1934, "Student" (Paper 27) used the results to estimate the numbers of genes affecting the trait. Although his results are probably just as unreliable as others, his presentation and approach to the problem are of interest. In the final paper, Thoday (Paper 28) outlines a method for identifying the effects and positions of genes influencing quantitative traits. Indeed, it is an attempt to describe the formal genetics of a quantitative trait.

The overall coverage is bound to be patchy, and there may be whole areas omitted. Early experimental papers tended to be very detailed and lacked any theoretical basis. There were also many theoretical developments that could have been covered, particularly on linkage and on finite populations, as well as experiments testing predictions in relation to population size. The major topic of changing rates of evolution, on which much heat is expended, has also been ignored. Here the intention has been to include not just the important topics, but also papers from as many as possible of the important workers on selection for quantitative traits.

For further reading and references, the textbooks by Falconer (1981) and Mather and Jinks (1982) and the symposium volumes edited by Pollak et al. (1977) and Robertson (1980) are recommended, and there are many relevant papers in the Proceedings of the Second World Congress on Genetics Applied to Livestock Production (1982). A more complete review of texts in the general area of quantitative genetics is given in the introduction to Part I.

A criticism that can be leveled against quantitative genetics as a discipline, as opposed to other branches of genetics, is that it is simply a "black-box" approach. An individual or a population is described not in terms of its components, the genes and their biological actions, but in terms of, for example, input-output parameters such as the regression of progeny on parent performance or realized heritability. Some attempts can be made to describe the formal genetics—for example, in the approach made by Thoday—but if there are many loci, a complete description becomes a practical impossibility. Is the science of quantitative genetics and its application to problems of selection then of any value? It is, because predictions can be made from the "black-box" theory, they can be and have been tested by experiments, and animal and plant breeders have put them to practical use. It is hoped that the papers included in this volume will help to convince any skeptical readers.

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NATURE OF SELECTION RESPONSE